OCCASIONAL PAPERS

of the
MUSEUM OF NATURAL HISTORY
The University of Kansas
Lawrence, Kansas

NUMBER 100, PAGES 1-22 JUNE 16, 1982

PHYLOGENETIC RELATIONSHIPS OF THE COLUBRID SNAKES OF THE GENUS *ADELPHICOS* IN THE HIGHLANDS OF MIDDLE AMERICA

BY

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Snakes of the genus *Adelphicos* are widely distributed in southern México and northern Central America. *Adelphicos quadrivirgatus* occurs on the Atlantic versant and coastal plain from the foothills of central Veracruz, México, through Guatemala and Belice, exclusive of the outer Yucatán Peninsula; and on the Pacific versant from central Oaxaca, México, into central Guatemala. This species ranges from about sea level to 1400 m in a variety of habitats including lowland rainforest and quasirainforest, lower montane dry forest, and lower montane wet forest (for chorography of vegetation complexes see Stuart, 1966:692). *Adelphicos quadrivirgatus* is distinctive from all highland populations of *Adelphicos* by having chin shields that are greatly expanded toward the lip and in the anterior position of the first ventral that is generally at the level of the posteriormost labials (Smith, 1942).

Disjunct populations of *Adelphicos* occur in the Middle American highlands at elevations of 1200-2200 m on the Sierra Madre de Chiapas in extreme southeastern Oaxaca, the Meseta Central of Chiapas, the Sierra de los Cuchumatanes, and the Sierra de las Minas and neighboring mountains in Guatemala (Fig. 1). The various allopatric populations of highland *Adelphicos* are isolated in humid pine-oak or cloud forests and are differentiated from each other in characters of squamation, color, pattern, osteology, and body proportions.

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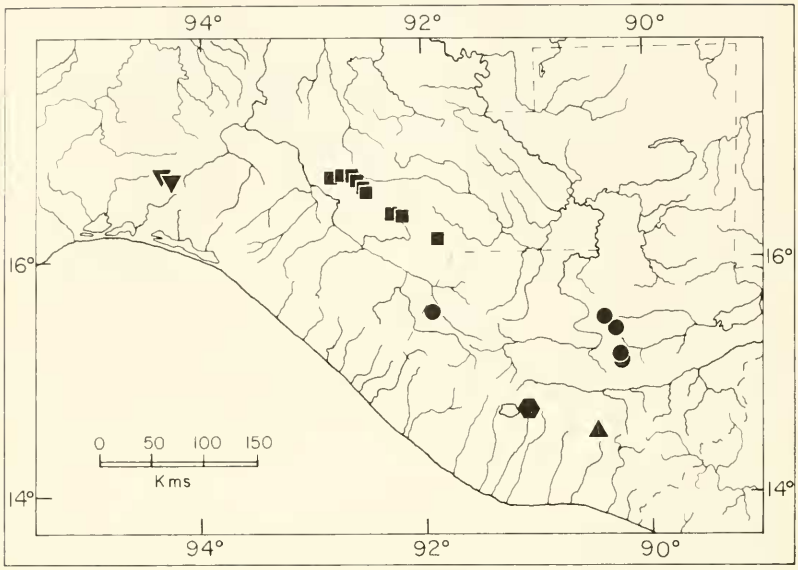

FIG. 1. Distribution of highland *Adelphicos* in southern México and Guatemala. Symbols representing the following: inverted triangles, *A. latifasciatus;* squares, *A. nigrilatus;* circles, *A. veracpacis;* triangle, *A. daryi;* hexagon, unallocated specimen.

Some of these populations have been recognized previously as subspecies of *A. veraepacis.* However, we believe these populations have diverged sufficiently from each other to merit recognition as species. We provide diagnoses, descriptions, and a key for all known members of the highland group. Our phylogenetic analysis was determined in the manner suggested by Wiley (1981) using other burrowing xenodontine colubrids (especially *Geophis*) as the outgroup. Although highland *Adelphicos* are not common in collections, we are fortunate in having observed all four species in the field. We examined a total of 129 snakes: 4 *A. latifasciatus*, 58 *A. nigrilatus*, 59 *A. veraepacis*, and 8 of the new species described herein. These species constitute a monophyletic lineage referred to as the *veraepacis* group, endemic to the Middle American highlands.

We measured cephalic scales to the nearest 0.1 mm using an ocular micrometer. Measurements were taken along or perpendicularly to the long axis of the scale. Body lengths were taken to the nearest mm using a meter stick. In comparing the relative eye sizes of the various species we took the horizontal distance across the eye from the posterior edge of the loreal to the level between the postoculars. This distance was divided into the snout length, the distance from the anterior edge of the eye to the front face of the rostral.

The first plate bordered on both sides by the first row of dorsals was considered to be the first ventral (Dowling, 1951). We use the term cephalic index to denote head width/head length × 100.

Three of the highland populations have been named. *Adelphicos veraepacis* Stuart was based on four specimens from Alta Verapaz, Guatemala; *A. nigrilatus* Smith was proposed for specimens from the Meseta Central of Chiapas, México; and *A. latifasciatus* Lynch and Smith was based on a single specimen from the Sierra Madre north of Zanatepec, Oaxaca, México. The population from the mountains southeast of Guatemala City is represented by a series of eight specimens and is unnamed. We propose that this unique snake be known as

Adelphicos daryi, new species

Figs. 2, 4—6

Holotype.—KU 187260, an adult female, from San Jorge Muxbal, 5.5 km W San José Pinula, Department of Guatemala, Guatemala, elevation 1844 m, collected by J. A. Campbell on 11 July 1980, original number JAC 5305.

Paratypes.—UTA R-5743, 5897, 6223, 7129, KU 187259, 190886, female topotypes taken 30 May 1976, July 1976, November 1976, 12 September 1977, June 1980, and August 1980, respectively, at elevations of 1829 to 2134 m by J. A. Campbell, L. S. Ford, and P. Castillo; KU 187258, male topotype, taken September 1979 at 2134 m by P. Castillo.

Diagnosis.—The new species is a member of the *veraepacis* group that can be distinguished from all other members of the group by its large size, females attain lengths of at least 574 mm and males probably exceed 400 mm; broad frontal plate, at least as broad as long; dorsal coloration dark brown suffused with black; relatively small eye, contained 2.7—3.2 times in the snout length; low number of dentary teeth, 8—9 (mode 9).

It usually may be distinguished from *A. veraepacis* and *A. latifasciatus* by its low number of ventrals, 120 in male, 128—132 in females, opposed to 120—133 and 128 in males, and 132—142 and 133—138 in females, respectively. The male possesses 28 subcaudals, whereas males of *A. veraepacis* have 29—41 and *A. latifasciatus* have 46—51. The number of subcaudals, 19—22, distinguishes female *A. daryi* from *A. veraepacis* (24—31) and *A. latifasciatus* (37—41). The modal number of palatine teeth is 7 in *A. daryi* and 8 and 9 in *A. nigrilatus* and *A. latifasciatus*, respectively.

Description of holotype.—An adult female, 487 mm in total length; tail length 48 mm (9.9% of total); head length 16.3 mm from front face of rostral to posterior end of mandible; head width

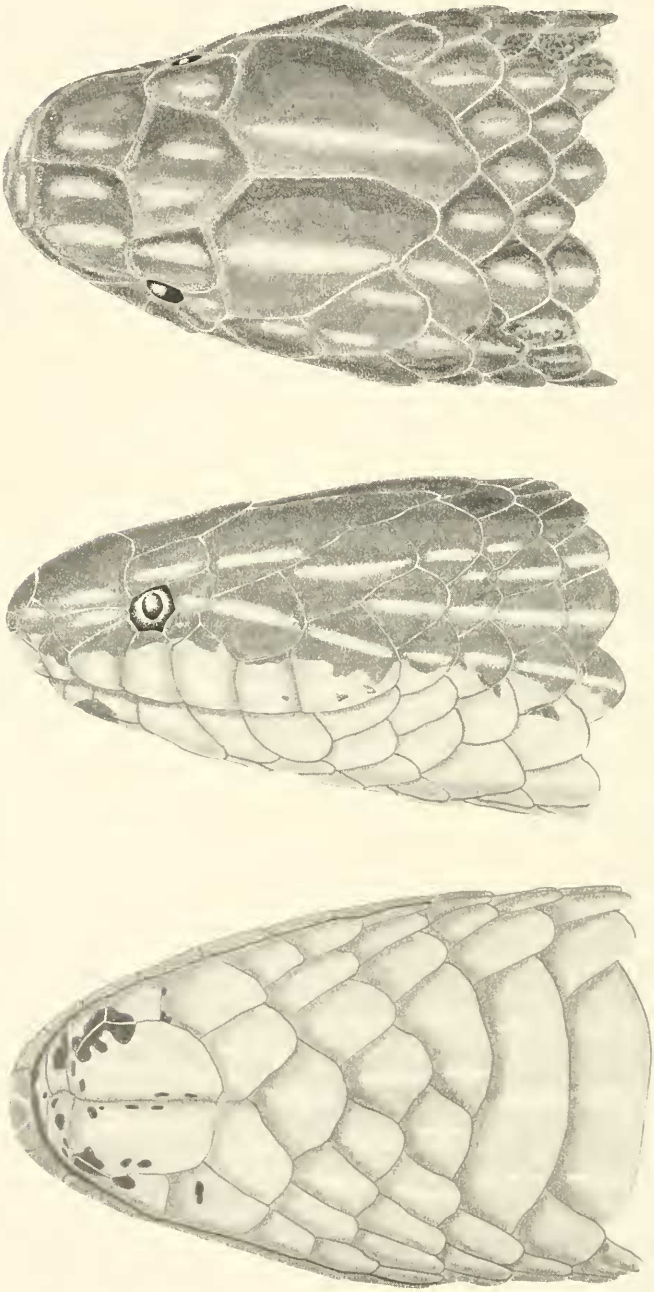

FIG. 2. Dorsal (upper), lateral (middle), and ventral (lower) aspects of the head of *Adelphicos daryi* (holotype, KU 187260).

11.2 mm at broadest point at the rictus; head moderately distinct from neck; snout rounded in dorsal view; eye small, snout 3.0 times as long as horizontal distance across eye; pupil round; rostral about 1.2 times broader than high; internasals 1.4 times wider than long, contacting anterior and posterior nasals laterally; prefrontals large, slightly longer than wide, contacting posterior nasal and loreal laterally; median prefrontal suture 0.6 times as long as frontal; frontal as broad as long; parietals about 1.6—1.8 times longer than wide, median suture 1.1 times frontal length; nostrils located in anterior nasal; loreal about equal to combined length of nasals; preocular absent; supraocular large, 1.1 times longer than loreal; two postoculars; temporals 1—1, separating supralabials 6 and 7 from parietal; supralabials 7/7, 1 contacting nasals, 2 contacting postnasal and loreal, 3 contacting loreal, 3 and 4 entering orbit, 5 and 6 contact anterior temporal, 6 largest and contacting posterior temporal; mental 3.8 times broader than long, separated from chin shields by first infralabials which contact each other along midline; chin shields well developed, about twice as long as wide and not extending to border of lip; posterior chin shields not differentiated from gulars; anterior chin shields separated from first ventral by four gulars; infralabials 7/7, 1—4 contacting anterior chin shields, fourth largest; unreduced dorsal scales in 15 smooth rows throughout length of body; dorsal scales in 6 rows at the level of the tenth subcaudal; no apical pits apparent; ventrals 133; anal divided; subcaudals 21, paired; anal glands paired, extending 2 subcaudals.

Coloration in preservative (alcohol after formalin): dorsal ground color brown strongly suffused with black; black lateral stripe on upper half of scale row 1, all of 2, and lower three-fourths of row 3; paravertebral stripes on upper part of fifth and lower part of sixth row; middorsal black stripe on vertebral row; ventrals pale yellow with dark anterior and outer borders; subcaudals yellow with black outside borders and darkly pigmented along midventral sutures forming stripe; top of head dark brown extending to upper part of supralabials; gular area yellow with little mottling on mental, first three pairs of infralabials, and anterior portion of chin shields. These colors, taken from the freshly preserved specimen, generally agree with notes from life, except for the ventrals which were bright yellow.

Variation.—The following data were taken from the holotype and seven paratypes. The total body length in females is 395—574 mm with the tail comprising 9.6—10.8% ($\bar{x}$ = 10.1%) of the total length. Four of the six females exceed 500 mm. The number of ventrals is 128—133 ($\bar{x}$ = 130.7) and subcaudals, 19—22 ($\bar{x}$ = 20.6). The single male is 339 mm in total length with the tail comprising 15.0% of the total length. It has 120 ventrals and 28 subcaudals.

The head length is 3.3—3.9 mm ($\bar{x} = 3.6$) of the total length and the cephalic index is 61—69 ($\bar{x} = 66.0$). The distance across the eye is contained from 2.7—3.2 ($\bar{x} = 3.1$) times in the snout length. The frontal is 1.0—1.1 times broader than long. The supralabials are 7/7 in all but one specimen (UTA R-6223) which has 6 on one side. The infralabials are 7/7. The number of teeth is 7—10 on the maxillary, 7—8 on the palatine, 13—17 on the pterygoid, and 8—9 on the dentary.

The ground color of *A. daryi* is brown strongly suffused with black. The lateral stripes extend along scale row 2 and the upper and lower parts of scale rows 1 and 3, respectively. The unbroken paravertebral stripes extend along the upper part of row 5 and lower part of 6. The vertebral stripe is obscured by dark pigment in one specimen, only barely discernible in two, and clearly defined in one. The ventrals are yellow with black-edged outer and anterior margins; there is no darkening midventrally. The subcaudals are light yellow with dark brown or black outer borders and a distinct black midstripe on the undersurface of the tail. The gular area is immaculate, but the area near the sutures of the anteriormost three infralabials, mental, and chin shields is mottled with brown or black.

Distribution.—Known only from the humid pine-oak forest fringing the Las Nubes block in the southeastern Guatemalan highlands at 1829 to 2134 m (Fig. 1).

Etymology.—The specific name is a patronym for the late Mario Dary Rivera, outstanding Guatemalan biologist and conservationist.

Specimens examined.—(8) The type series constitutes the only known specimens of this species.

Adelphicos veraepacis

Figs. 4—6

1941 *Adelphicos veraepacis* Stuart, Occ. Pap. Mus. Zool. Univ. Mich., 452:5. Type locality: Finca Samac, 7 km W Cobán, 1500 m, Alta Verapaz, Guatemala. Holotype: UMMZ 89073, an adult male, coll. L. C. Stuart, 21 April 1938.

1942 *Adelphicos veraepacis veraepacis* Smith, Proc. Rochester Acad. Sci., 8:180.

Diagnosis.—A moderately large *Adelphicos*, females to 461 mm and males to 372 mm total length, possessing a unique combination of characteristics: females may be distinguished from all *A. daryi* and most *A. nigrilatus* by having a higher number of ventrals (132—142); males possess 29—41 subcaudals and females have 24—31, distinguishing them from *A. daryi* and *A. latifasciatus* which possess fewer and more subcaudals, respectively. The dark brown or gray dorsal coloration can be confused only with *A. daryi*, but the scales

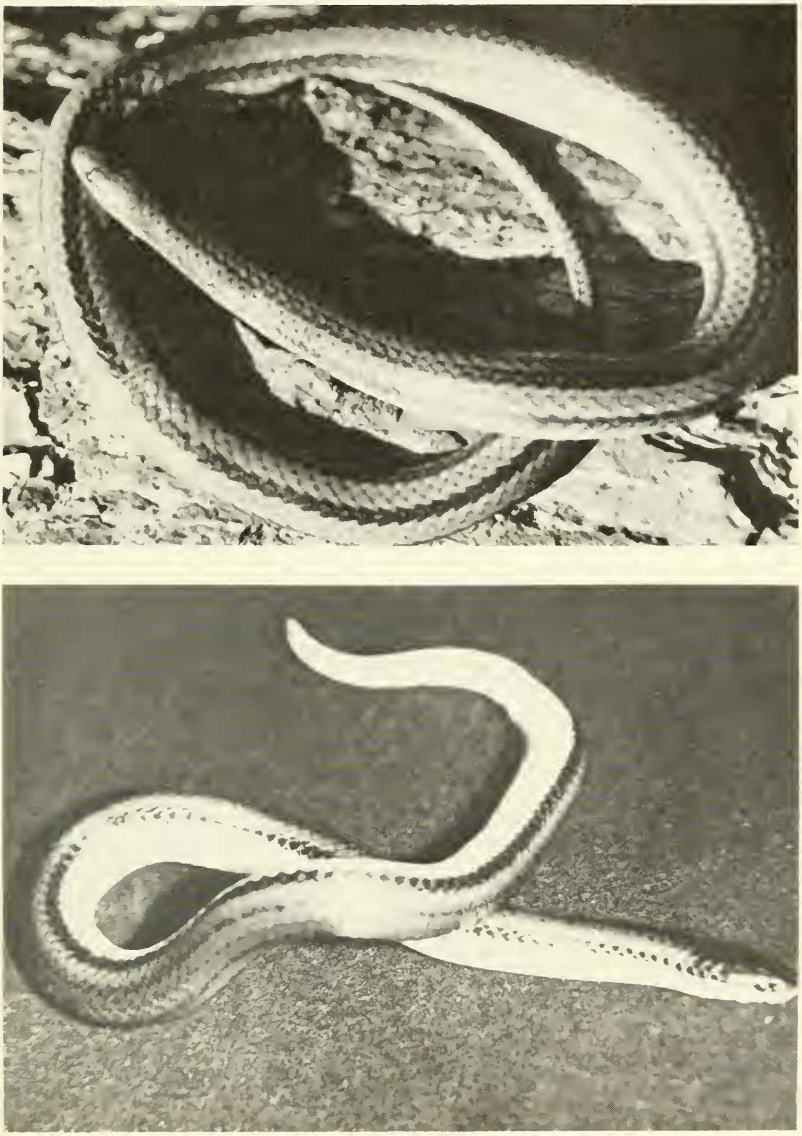

FIG. 3. Upper, *Adelphicos latifasciatus*—Cerro Baúl, Oaxaca, México (JAC 5539); lower, *A. nigrilatus*—6.9 mi SE Teopisca, Chiapas, México (UTA R-2452).

of the first scale row are not light posteroventrally or only slightly so, in contrast to the boldly defined pale spots in *A. daryi* (Fig. 5). The dorsolateral stripes generally are not continuous and involve no more than the edges of two adjacent scale rows. The anterior

edges of the ventrals are darkly pigmented like *A. daryi*, but there is a heavy concentration of dark pigment midventrally. This species may be distinguished from *A. daryi* by possessing a relatively larger eye that is contained 1.3—2.6 times in the snout length.

Variation.—In a sample of 29 males, one exceeds 350 mm (356 mm) and 14 are between 300 and 350 mm. Females are larger, but the largest female, 524 mm in total length, is far greater in length than other specimens. In a sample of 24 specimens, nine are between 300 and 350 mm, eight lie between 350 and 400 mm, and two exceed 400 mm. Males have 120—133 ($\bar{x} = 126.0$) ventrals; relative tail lengths of adults are 14.5—19.4% ($\bar{x} = 16.5$) and 10.0—13.4% ($\bar{x} = 11.9$) of the total for males and females respectively. The frontal is 0.67—0.94 ($\bar{x} = 0.84$) times as broad as long, and the average cephalic index is 61. The eye size is contained 1.4—2.6 ($\bar{x} = 2.1$) times in the snout length.

Specimens from the Montañas de Cuilco of Guatemala differ in minor respects of color and pattern from snakes collected in Alta and Baja Verapaz. Although these differences distinguish snakes from the two regions from each other in most instances, these snakes are so similar in other respects we feel they do not warrant specific recognition.

Snakes from the highlands of Alta and Baja Verapaz are generally dark brown. Specimens may be so dark as to partially obscure the stripes. The lateral stripes usually extend along scale row 2 and the upper and lower parts of scale rows 1 and 3, respectively. In about half of the specimens the lateral stripe extends from the outer edge of the ventrals to the lower half of scale row 3 with only a small amount of or no light coloration on scale row 1, a condition not noted in any specimen from elsewhere. In no snakes from this region does the lateral stripe extend to scale row 4. The paravertebral stripes are invariably broken and located on the upper part of scale row 5 and lower part of scale row 6. The vertebral stripe is broken in about half of the specimens. The yellow ventrals are heavily pigmented along the midline producing a series of more or less triangularly shaped blotches with their apices produced posteriorly. The subcaudals are mostly dark with no well-defined midstripe. The gular area and chin shields are heavily mottled. The upper one-fourth to one-third of the supralabials is black and dark pigment may extend down the intrasupralabial sutures to the margin of the lip.

Specimens from the Montañas de Cuilco are generally medium to dark brown and are frequently paler in over-all appearance than the snakes from Alta and Baja Verapaz. The lateral stripes are usually located on scale row 2 and the adjacent parts of scale rows 1 and 3 respectively, but in eight of 37 specimens the lateral stripe extends up to the lower part of scale row 4, a condition not present

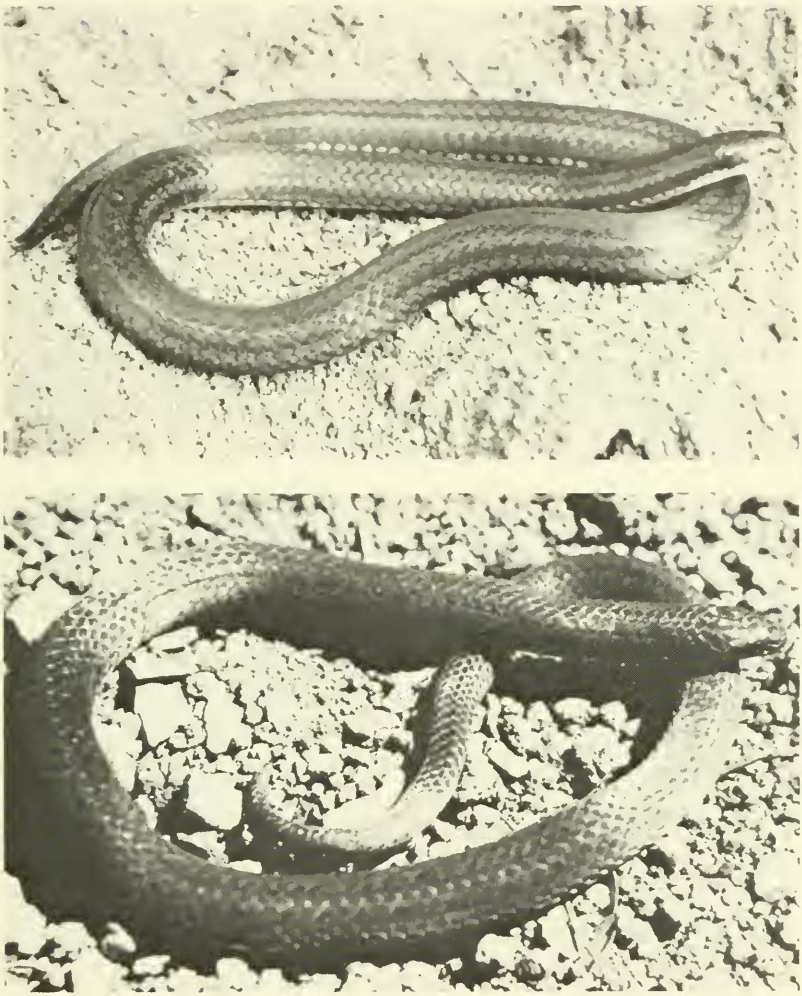

FIG. 4. Upper, *Adelphicos daryi*—San Jorge Muxbal, Guatemala, Guatemala (KU 187260, holotype); lower, *A. veraepacis*—W slope Cerro Verde, Baja Verapaz, Guatemala (KU 190891).

in specimens from other parts of the range. The paravertebral stripes are usually continuous (broken in only one specimen) and variably located on parts of scale rows 5 and 6 (11 specimens), 6 (13), 6 and 7 (7), or 5, 6, and 7 (2). The vertebral stripe is unbroken and discernible in all specimens except several that appear to have been darkened by preservative. The ventrals are yellow with dark brown or black outer edges and with little to moderate amounts of pigment along their anterior borders. There is no tendency for darkening along the ventral midline. The subcaudals are

pale with black pigment along their inside borders forming a midventral stripe on the tail. The gular area and chin shields are usually immaculate, but a small amount of mottling is occasionally present. Black pigment may barely encroach on the upper part of the supralabials.

Etymology.—The specific name is in reference to the department of Alta Verapaz, Guatemala, from which the type specimens originated.

Distribution.—The northern mountains of Guatemala: the Montañas de Cuilco, the Sierra de las Minas and neighboring mountains, and probably the Sierra de los Cuchumatanes, from 1200 to 2200 m elevation in cloud and pine-oak forests (Fig. 1). Stuart (1943b) reported a specimen without precise locality data that may have originated from either the Sierra de los Cuchumatanes or the Guatemalan Plateau, but he favored the former.

Specimens examined.—(59) GUATEMALA: *Alta Verapaz:* Finca Chichén [FMNH 109861 (paratype), UMMZ 89074-75 (paratypes)]; *Baja Verapaz:* Cerro Quisís (KU 190890, UTA R-7082); Cerro Verde (KU 190891, 190894-95, UTA R-6542, 6551, 6571, 6584, 7081, 7083); El Bagasal (KU 187320); near La Unión Barrios (KU 190889, 190892-93, UTA R-7084); 7.7 km SSE Purulhá (UTA R-6479); 1.6 km SE Purulhá (UTA R-8841); *Huehuetenango:* Paraíso [UMMZ 127233(17), 127234-37, 127238(4), 127239(2), 127240(3), 127241(2), 127266-70]; *No Specific Locality:* (UMMZ 90239).

Adelphicos nigrilatus

Figs. 3, 5—6

1942 *Adelphicos veraepacis nigrilatus* Smith, Proc. Rochester Acad. Sci., 8:182. Type locality: San Cristóbal de las Casas, Chiapas, México. Holotype: USNM 137219 (formerly EHT-HMS No. 15335), coll. H. Devlin Thomas.

Diagnosis.—The most variable member of the *veraepacis* group; most easily distinguished from *A. daryi* and *A. veraepacis* by its bright orange, red, or pale brown ground color. The vertebral scale row is pale in coloration when the middorsal stripe is absent, thereby distinguishing this species from *A. daryi* and *A. veraepacis;* when present, it involves only the vertebral scale row, thereby distinguishing this species from *A. latifasciatus.* In most specimens the venter is unpigmented, distinguishing *A. nigrilatus* from *A. daryi* and *A. veraepacis,* whereas in a few specimens the possession of heavy pigmentation midventrally distinguishes *A. nigrilatus* from *A. latifasciatus,* and it lacks the dark anterior edging characteristic of *A. daryi* and *A. veraepacis. Adelphicos nigrilatus* may be distinguished from *A. latifasciatus* by having fewer subcaudals (21—26

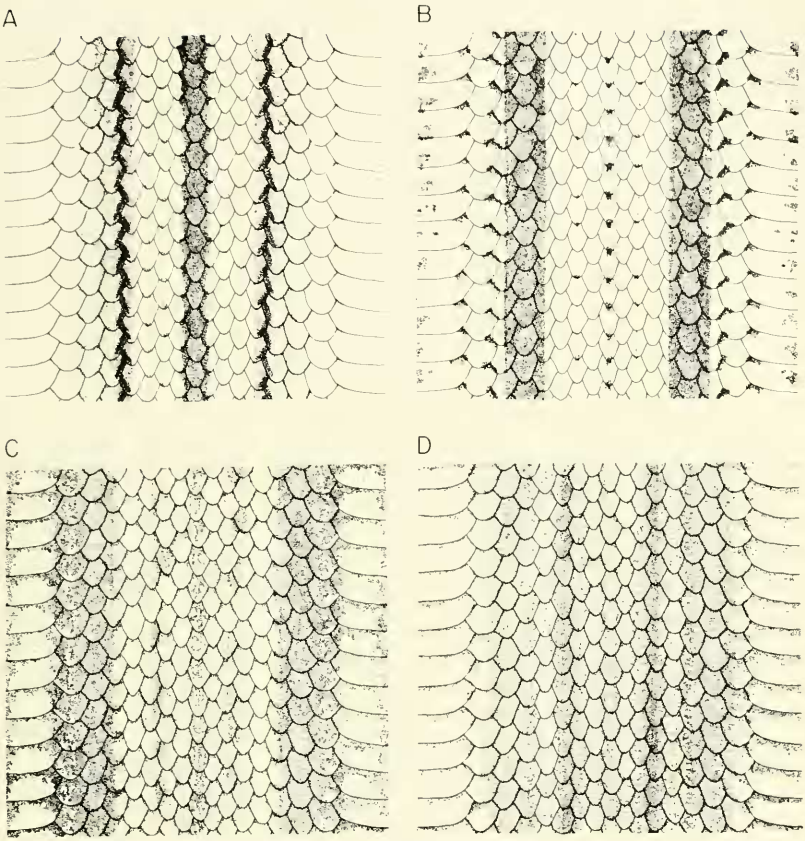

FIG. 5. Patterns of the highland species of *Adelphicos:* a) *A. latifasciatus* from Cerro Baúl, Oaxaca, México (UTA R-8794); b) *A. nigrilatus* from 6.8 mi ESE San Cristóbal de las Casas, Chiapas, México (UTA R-8837); c) *A. veraepacis* from Cerro Quisís, near La Unión Barrios, Baja Verapaz, Guatemala (UTA R-7082); and d) *A. daryi* from San Jorge Muxbal, Guatemala, Guatemala (KU 187260, holotype).

and 26—36 in males and females, respectively) and relatively shorter tail in males and females, 13.5—18.9% (16.2%) and 10.3—12.9% (11.6%) of the total length, respectively. Female *A. nigrilatus* generally have fewer ventrals than do those of *A. veraepacis* and *A. latifasciatus.*

Variation.—Females are larger than males; in a sample of 25 females, seven were between 250 and 300 mm, five between 300 and 350 mm, one between 350-400 mm, and one was 451 mm in total length. In a sample of 32 males, eight were between 250-300 mm, the largest being 293 mm. There are 113—128 ($\bar{x} = 118.1$) ventrals in males and 123—135 ($\bar{x} = 127.7$) in females. The frontal

width is from 0.67 to 0.94 ($\bar{x}$ = 0.82) of the frontal length; the average cephalic index is 58. The eye is contained 1.4—2.6 ($\bar{x}$ = 2.0) times in the length of the snout.

The ground color of this species is generally bright orange in life, fading to a pale beige or tan in preservative. Black lateral stripes frequently involve the upper portion of scale row 2, all of 3, and the lower portion of scale row 4 (33 of 53 specimens), but also may be located on scale row 3 (7), upper 3 and lower 4 (6), upper 1, 2, lower 3 (3), upper 1, 2, 3, lower 4 (2), upper 3, 4, lower 5 (1). The paravertebral stripes may be absent (16 or 53 specimens), but usually are present on scale row 6 (18), upper 6 and lower 7 (10), upper 5 and lower 6 (7), 5 (1), or lower 7 (1). The vertebral stripe is absent in 11 specimens, present but broken in three, and unbroken in 39.

Etymology.—The name *nigrilatus* is derived from the Latin *nigri* meaning black, and *latus* meaning side, and refers to the distinctive lateral stripes on the body.

Distribution.—The Meseta Central of Chiapas, México, from the vicinity of San Cristóbal de las Casas southeastward almost to the Guatemalan border, from 2200 to 2500 m elevation in cloud and pine-oak forests (Fig. 1).

Specimens examined.—(58) MÉXICO: *Chiapas:* San Cristóbal de las Casas [USNM 137219 (holotype), CAS 20617 (paratype), FMNH 100285-91 (paratypes), MCZ 56017 (paratype), AMNH 66961, UF 42073]; 4 mi SE San Cristóbal de las Casas (AMNH 99981), 6.8 mi ESE San Cristóbal de las Casas (UTA R-8837), 7.3 mi E San Cristóbal de las Casas (AMNH 102917), 8.2 mi E San Cristóbal de las Casas [UMMZ 119761(6), 121536(2)], 3 mi W San Cristóbal de las Casas (AMNH 93317), 15 mi W San Cristóbal de las Casas (UMMZ 94595), 9 mi NW San Cristóbal de las Casas (MVZ 109478), 15.5 mi E San Cristóbal de las Casas (UTA R-2514), 9 km W San Cristóbal de las Casas (CAS 145203), 4.0 km W San Cristóbal de las Casas (KU 37594), 4.3 km W San Cristóbal de las Casas (MVZ 144524), 10 km SE San Cristóbal de las Casas (KU 129230), 6.5 mi SE San Cristóbal de las Casas (LACM 58124-27, TCWC 30410-12, UMMZ 94593-94), 6.8 mi SE San Cristóbal de la Casas (LACM 58128-29, 58149, TCWC 30414-18), 7.4 mi SE San Cristóbal de las Casas (UMMZ 126171), 13 mi E Las Rosas (TCWC 12801); 6.9 mi SW Teopisca (UTA R-2452); 11.2 mi S Teopisca (LACM 58899); 24.1 mi SE Teopisca (TCWC 30413); 1.0 mi E Tulanca on Mex Hwy 190 (UTA R-8839-40), 1.1 mi E Tulanca on Mex Hwy 190 (UTA R-8838); Puente de Chamic (UCM 19039); 18 km E Mex Hwy 190 on road to Lago Montebello (MVZ 112403).

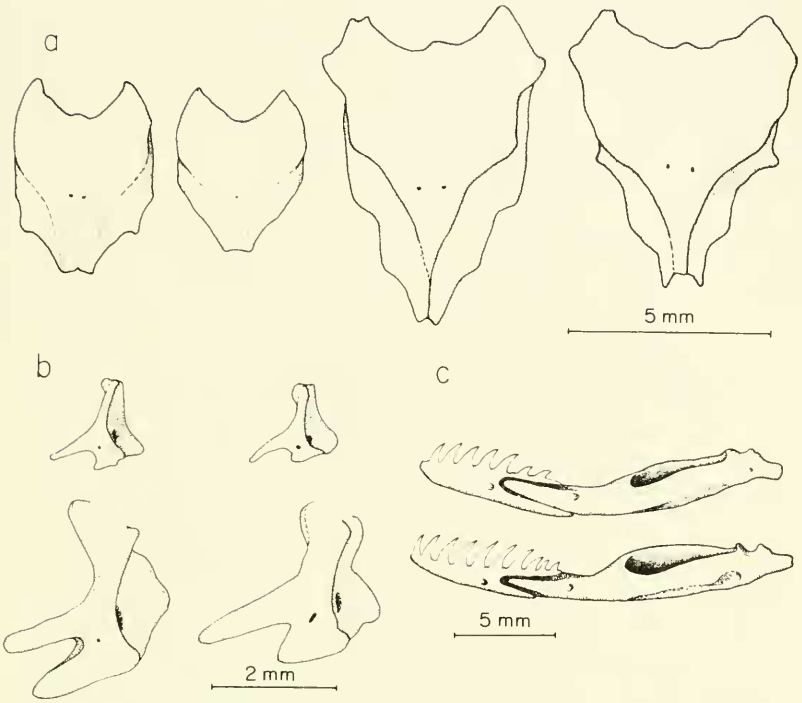

FIG. 6. A) From left to right, dorsal views of the parietals of *Adelphicos latifasciatus* (UTA R-6213), *A. nigrilatus* (UTA R-2514), *A. veraepacis* (UTA R-7083), and *A. daryi* (UTA R-5897, paratype); B) Clockwise from upper left, lateral views of the prefrontals of the same specimens listed above; C) Lateral views of the mandibles of *A. daryi*, UTA R-5897 (upper), and *A. veraepacis*, UTA R-7083 (lower).

Adelphicos latifasciatus

Figs. 3, 5—6

1966 *Adelphicos veraepacis latifasciatus* Lynch and Smith, Trans. Kansas Acad. Sci., 69:66. Type locality: Sierra Madre north of Zanatepec, Oaxaca, México. Holotype: UIMNH 56147, coll. Thomas MacDougall, 6—12 Sept. 1963.

Diagnosis.—The species may be distinguished from all other members of the *veraepacis* group by the high number of subcaudals in males (46—51) and females (37—41), its relatively long tail comprising 20.4—22.3% and 14.6—15.6% of the total length in males and females respectively, and its broad middorsal stripe that includes the vertebral and adjacent halves of the paravertebral scale rows. The modal number of teeth tends to be more (11 maxillary, 11 dentary, 9 palatal, and 18 pterygoid) than in the other species. It can be distinguished from *A. daryi* and *A. veraepacis* by its pale

to reddish brown ground color. It differs from *A. daryi*, *A. veraepacis*, and most *A. nigrilatus* by lacking paravertebral stripes and having an unpigmented venter. In *A. latifasciatus* the lateral stripe involves scale row 3 and adjacent halves of scale rows 2 and 4, whereas in *A. daryi* and *A. veraepacis* the stripe includes scale row 2 and adjacent portions of scale rows 1 and 3.

Variation.—Total lengths in two males are 310 and 333 mm, in three females the total length is 323-437 mm; ventrals are 125—128 ($\bar{x} = 126.5$) in males, 133—138 ($\bar{x} = 135.7$) in females; the frontal is 0.82—1.00 ($\bar{x} = 0.87$) times as broad as long. The average cephalic index is 60 and the eye is contained 2.2—3.2 ($\bar{x} = 2.6$) times in the length of the snout.

In four specimens of *A. latifasciatus* from Cerro Baúl, Oaxaca, the ground color is reddish to pale brown, the lateral stripes involve scale row 3 and adjacent parts of rows 2 and 4. Paravertebral stripes are absent, and the vertebral stripe includes the vertebral and half of the paravertebral scale rows. The top of the head is dark brown, extending to the upper part of the supralabials. The gular area and ventrals are immaculate except for the pale mottling on the outer portion of the ventrals. The subcaudals are pale with a midventral stripe along their median sutures. Except for their pale dorsal ground color, these specimens agree in aspects of pattern and color with the description given for the holotype (Lynch and Smith, 1966). The terms "dark" and "pale" are relative and we suspect from viewing the photograph of the holotype (Lynch and Smith, 1966:67) that even the ground color is in agreement.

Etymology.—The name *latifasciatus* is derived from the Latin *lati*, meaning broad or wide, and *fasciatus*, meaning a band, and refers to the distinctive broad dorsal stripe.

Distribution.—The cloud forest on the western portion of the Sierra Madre de Chiapas in Oaxaca, México, at elevations of 1500 to 1900 m.

Specimens examined.—(*4*) MÉXICO: *Oaxaca:* Cerro Baúl (UTA R-6213, 8793-94, JAC 5539).

OSTEOLOGICAL DIFFERENCES AMONG HIGHLAND ADELPHICOS

Many osteological differences exist among the highland species of *Adelphicos*. We have examined skeletal material of the following: *A. latifasciatus* (UTA R-6213, JAC 5539), *A. nigrilatus* (UTA R-2514, 8840), *A. veraepacis* (UTA R-7081-83, KU 187321), and *A. daryi* (UTA R-5743, 5897).

Premaxillae.—The leading horizontal edge of the premaxilla is flared in *A. daryi*, but not in the other species. The configuration of the premaxilla and nasals causes distinct differences in head

shape: in lateral profiles the snouts of *A. latifasciatus* and *A. nigrilatus* are acuminate, *A. veraepacis* is subtruncate, and *A. daryi* is truncate.

Prefrontals.—The extent to which the prefrontal is in contact

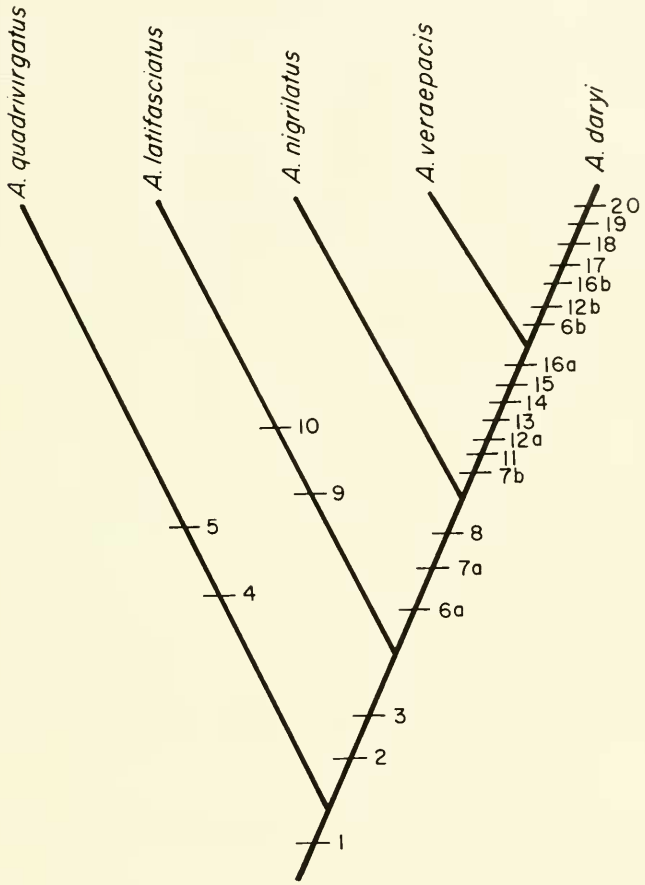

FIG. 7. A theory of the relationships of snakes of the *veraepacis* group of *Adelphicos*. Numbers refer to the following characters: 1) single sulcus; 2) broad lateral stripes; 3) increase in number of hemipenial spines; 4) enlarged chin shields; 5) position of first ventral; 6) subcaudals, a. decrease in number, b. extreme reduction; 7) a. venter with some pigmentation, b. anterior edges of ventrals dark; 8) decrease in number of teeth; 9) broad vertebral stripe; 10) loss of paravertebral stripe; 11) dark ground color; 12) lower arm of prefrontal well developed, a. lower arm less than ½ length of upper, b. lower arm ¾ to equal upper; 13) posterior median ridge on parietal and supraoccipital; 14) dorsolateral edges of parietal well defined; 15) large size; 16) profile, a. subtruncate, b. truncate; 17) greatly expanded hypapophyses in anterior trunk vertebrae; 18) stout teeth; 19) broad frontal; 20) flared premaxilla. See text for details.

with the maxilla varies from *A. latifasciatus* and *A. nigrilatus*, in which the anteriorly projecting lower arm of the prefrontal is poorly developed, to *A. daryi* in which the lower arm is almost equal to the length of the upper arm (Fig. 6). *Adelphicos veraepacis* has a lower prefrontal arm that is intermediate in length between that of *A. daryi* and the other species.

Frontals.—The frontals are broader than long in all species, but in *A. nigrilatus* they are relatively longer and more tapering posteriorly than in the other species.

Parietals.—Perhaps no character is more distinctive in these snakes than the condition of the parietal in adult snakes (Fig. 6). In *A. latifasciatus* and *A. nigrilatus* the parietal is broadest at about its midlength, whereas in *A. veraepacis* and *A. daryi* it is broadest anteriorly. It is broader in *A. daryi* than any other species, with well-defined, sharp, dorsolateral edges that are close together posteriorly. The parietal is slightly narrower in *A. veraepacis*, and the dorsolateral ridges may coalesce posteriorly. In both *A. latifasciatus* and *A. nigrilatus* the dorsolateral ridges are poorly defined and the parietal is flatter. In *A. daryi* and *A. veraepacis* the dorsolateral parietal ridges are distinctly raised posteriorly forming a median crest that extends through the supraoccipital, whereas in *A. latifasciatus* and *A. nigrilatus* no such crests exists.

Maxillae.—A comparison of the maxillae reveals *A. daryi* has a relatively stout maxilla, whereas in the other species it is not as stout nor as firmly articulated with the prefrontals and ectopterygoids.

Mandibles.—Several distinguishing characters concerning the mandibles exist for these species. The mandibles are more massive in the western species. This trend is particularly reflected in the stout splenial of *A. daryi*. The position of the mental foramen in reference to its distance from the anterior tip of the compound is less in *A. nigrilatus* and *A. veraepacis*.

Teeth.—The shape of the teeth is diagnostic for *A. daryi* which has short, stout teeth (Fig. 6). In the other species the teeth are longer, more slender, and more strongly recurved. Also, there are differences in the number of teeth. Variations in the number of maxillary teeth with the modal number in parentheses for *A. latifasciatus*, *A. nigrilatus*, *A. veraepacis*, and *A. daryi* are 11(11), 9—10(9), 8—10(9), and 7—10(9), respectively. The number of dentary teeth varies from 11—12(11), 10—11(10), 10—11(10), and 8—9(9); and the number of palatal teeth ranges from 9(9), 10—11 (10), 7(7), and 7—8(7) in the above species, respectively. There are 18—20(18), 14—20(16), 13—16(16), and 13—17(16) pterygoid teeth in these species, respectively.

Vertebrae.—The hypapophyses of the anterior trunk vertebrae are greatly expanded relative to the long axis of the body in *A.*

daryi but are not so expanded in the other species. The interhypapophyseal spaces of the anterior trunk vertebrae are about equal to or less than the hypapophyses in *A. latifasciatus*, *A. nigrilatus*, and *A. veraepacis*, whereas in *A. daryi* the spaces between the hypapophyses are only about half of the hypapophyses. If the subcaudals are an accurate indicator of the number of caudal vertebrae, the number in *A. latifasciatus* is far greater than in *A. daryi*, with *A. nigrilatus* and *A. veraepacis* possessing an intermediate number.

Adelphicos daryi has a comparatively inflexible skull that is more sturdily constructed than those of the other species of highland *Adelphicos*. The maxillary in particular is more firmly attached and has greater articulating surfaces with the prefrontal and ectopterygoid. The significance of these morphological traits might well be elucidated through a knowledge of the habits of these snakes. The skeletal characteristics and over-all size suggest that the diet of *A. daryi* may vary from that of other *Adelphicos*, which is composed largely of earthworms.

The following key will serve to distinguish the species of *Adelphicos*.

A KEY TO THE SPECIES OF *ADELPHICOS*

1a. Third infralabial absent or greatly reduced in size; chin shields greatly expanded toward lip ..... *A. quadrivirgatus*

1b. Third infralabial not so reduced; chin shields not expanded toward lip 2

2a. Subcaudals more than 42 in males and 32 in females; dorsal stripe involving paravertebral scale row; venter unpigmented ..... *A. latifasciatus*

2b. Subcaudals less than 42 in males and 32 in females; dorsal stripe, if present, involving vertebral scale row only; venter pigmented or not 3

3a. Venter unpigmented, or darkened only midventrally, anterior edges of ventrals not conspicuously darkened; ground color bright orange, red, or tan ..... *A. nigrilatus*

3b. Anterior edges of ventrals conspicuously darkened; ground color brown or gray 4

4a. Venter not darkened midventrally; ventrals 120 in single known male, 128—132 in females; subcaudals 28 in male, 19—22 in females; frontal at least as broad as long ..... *A. daryi*

4b. Venter darkened midventrally; ventrals 120—133 in males; 132—142 in females; subcaudals 29—41 in males, 24—31 in females; frontal generally longer than broad ..... *A. veraepacis*

DISCUSSION

The decision of whether or not to recognize allopatric popu-

lations as species is often questionable. We agree with Wiley (1981) that populations diagnosable without recourse to geographic data are indicative of independent evolution from their common ancestor. Further, we are in accord with the concept that an evolutionary species is a single lineage of ancestor-dependent populations that maintains its identify from other such lineages and that has its own evolutionary tendencies and historical fate (Wiley, 1978; modified from Simpson, 1961).

Highland populations of *Adelphicos* exhibit distinct phenetic differences so that discrimination between them is facile. Lynch and Smith (1966:69) were understandably conservative in their assessment of the status of *A. v. latifasciatus* because they had only the holotype on which to base their views. It was perhaps the uniqueness of the specimen that prompted them to speculate "the taxonomic rank—although . . . not the taxonomic validity—of *latifasciatus* remains in doubt." They were further hampered by the notion that *A. latifasciatus* and *A. nigrilatus* occurred in physiographic continuity. The highlands of southeastern Oaxaca are separated from the range of *A. nigrilatus* not only by the formidable barrier presented by the Río Grijalva entrenchment, but also by about 120 km of low and unsuitable habitat. We think it unlikely that the two will be found sympatrically.

On the basis of the salamander fauna, Stuart (1943a) divided the highlands of Guatemala into five biotic areas. These were subsequently more appropriately designated as "faunal areas" (Stuart, 1950). *Adelphicos veraepacis* occurs in three of these: the Cuchumatan, the Quecchian, and the Sierran. Later, Stuart (1954b) recognized the Esquipulan Biotic Area, to which *A. daryi* is apparently confined. *Adelphicos daryi* is isolated from *A. veraepacis* by the xeric lowlands of the Río Motagua Valley—the Zacapan Faunal Area of Stuart (1954a)—and the seasonally dry uplands of the Guatemalan Plateau that is covered largely by pine-oak forest—the Chimaltenangan Faunal Area of Stuart. The importance of the Guatemalan Plateau as a barrier to dispersal of mesophiles has been emphasized by Stuart (1951). The type locality of *A. daryi* is separated from the southwestern highlands and Plateau of Guatemala by the graben in which lies Guatemala City, the Las Vacas Valley, which scarcely exceeds 1500 m at the ridge separating the headwaters of the Río Las Vacas and Río Michatoya.

In Guatemala the most northerly mountain ranges block most of the precipitation. *Adelphicos veraepacis* occurs in localized areas of high rainfall. To the south *A. daryi* occurs in a localized area of humid pine-oak forest. As noted by Stuart (1954b), most of the southeastern highlands of Guatemala are subhumid; however in a few localized areas of high elevation the low temperatures greatly increase the relative humidity and heavy dews occur even

in the dry season resulting in much more mesic conditions than those at lower elevations. These "temperate-cold upland forests" (Stanley and Steyermark, 1945; Steyermark, 1950) are characterized by abundant epiphytes and a deep humus layer. Environmental conditions within this forest are similar to cloud forest (Stuart, 1954b).

With the possible exception of a few high ridges on the Las Nubes block about 10 km to the east of the type locality and on which *A. daryi* probably occurs, the type locality of *A. daryi* is far removed from other mesic forests. Inasmuch as all specimens of the type series of *A. daryi* were secured within close proximity of water and in heavy cover, it seems that this species is a mesophile preferring extremely humid conditions.

The region around San Jorge Muxbal was almost totally cleared of native vegetation during the period from 1974 to 1980; *A. daryi* may soon be eliminated from the area.

Highland species of *Adelphicos* occupy distinct physiographic regions drained by separate rivers or distinct portions of a drainage system. *Adelphicos latifasciatus* occupies a range drained by the Río Coatzacoalcos and Río Grijalva; *A. nigrilatus* by the Río Grijalva and Río Usumacinta; *A. veraepacis* by the Río Polochic and Río Usumacinta; and *A. daryi* by tributaries of the Río Pinula which drains into Lake Amatitlán. *Adelphicos daryi* is distinctive by being the only member of the *veraepacis* group inhabiting a Pacific drainage.

The level of endemism in the southeastern Guatemalan highlands is not high. It seems as though many species have not been isolated for sufficient time and/or have not been subjected to sufficiently strong selective pressures to reach a specific level of divergence. However, perhaps the most important contributing factor is the extremely limited distribution of isolated, high peaks with humid forests in the southeast. One salamander, *Pseudoeurycea expectata,* is endemic, and *A. daryi* is the first reptile reported whose range is confined to the southeastern highlands, although further investigations of disjunct populations occurring in the southeastern and southwestern highlands may reveal more endemics.

The dispersal of inhabitants of mesic highland forests in southern México and northern Central America was accounted for by altitudinal climatic fluctuations in the Pleistocene (Duellman, 1960). Stuart (1950) suggested that a combination of world cooling and the extensive uplift in Nuclear Central America caused the herpetofauna of the region to diverge into highland and lowland groups. The distributions (Fig. 1), characteristics, and hypothesized relationships (Fig. 7) of the highland species of *Adelphicos* suggest that their ancestor probably originated in the northwestern mountains of Nuclear Middle America subsequent to the Pliocene orog-

eny that split off highland and lowland stocks. According to our concept of their relationships, *A. latifasciatus* is the most primitive species and progressively more derived species are found to the east of its range. It follows that dispersal and subsequent speciation has proceeded from extreme southeastern Oaxaca eastward. It seems probable that the ancestral populations of *A. daryi* gained access into the southeastern Guatemalan highlands via the Guatemalan Plateau during periods of Pleistocene climatic depression when more mesic conditions prevailed. On the basis of suggestive physiographic features, Stuart (1954b) hypothesized that the southeastern highlands were considerably more humid in the past than at present, a conclusion that is borne out by zoogeographic patterns of the herpetofauna.

Stuart (1951) did not report *Adelphicos* from the southwestern Guatemalan highlands, and the genus is absent from most of the Guatemalan Plateau. However, a specimen (UMMZ 127837) from the highlands of Chimaltenengo establishes the presence of the genus in at least one restricted area, and at once creates a problem and suggests an explanation. The Chimaltenengan specimen lends evidence that the region was considerably more mesic in the past allowing for dispersal of mesophiles and that the ancestor of *A. daryi* could have entered the Las Nubes region via the Guatemalan Plateau. However, *A. daryi* most closely resembles *A. veraepacis* and the Chimaltenengan specimen appears to have its affinities with *A. nigrilatus*. Although it is a female possessing 135 ventrals, the upper limit for *A. nigrilatus*, this specimen agrees well in other characteristics with *A. nigrilatus*. Most notably, it has a light orange ground color, an immaculate venter, and lateral stripes on the upper part of scale row 2, all of 3, and the lower part of row 4. On the basis of this single specimen and because of its seemingly puzzling distribution, we are hesitant to assign it to *A. nigrilatus*. The status of this isolated highland population hopefully will be clarified by the collection of additional material.

The highlands of the Meseta Central of Chiapas, Sierra de los Cuchumatanes, and the Chuacús-Minas-Mico range have continued to increase in elevation up to the present time producing severe rain-shadow conditions in the interior valleys (Stuart, 1954a) and having a drying effect on the Guatemalan Plateau in general. It has been suggested that the Las Nubes region reached a high elevation at about the same time as the southern volcanic highlands, the southwestern highlands, and the Sierra de los Cuchumatanes (Stuart, 1954b). Today, some populations of highland *Adelphicos* are isolated by portions of Stuart's (1954) subhumid corridor. The range of *A. daryi* is cut off to the north by the dry Río Motagua and Río Negro valleys, which are covered with "desert-chaparral" (Steyermark, 1950). *Adelphicos latifasciatus* is isolated by the

xeric Middle Grijalva Valley to the east-northeast that supports a vegetation of savanna, dry forest, and brushland (Miranda, 1952; Stuart, 1954a).

The Quecchian and Cuchumatan populations of *A. veraepacis* are weakly differentiated from one another. These two populations are isolated from each other by the deeply entrenched Río Negro gorge, but the capture of the upper course of the Río Polochic by the Río Negro has been verified (Sapper, 1937), and may have been the basis for the vicariance event that separated them. The weak level of divergence between the two populations suggests that their separation was recent relative to that between *A. veraepacis* and *A. daryi*.

ACKNOWLEDGMENTS

We thank the officials of the Instituto Nacional Forestal (INAFOR) in Guatemala and the Dirección General de la Fauna Silvestre in México who kindly issued collecting permits. For allowing us to examine material in their care we are indebted to C. W. Myers (AMNH), R. C. Drewes and A. E. Leviton (CAS), C. J. McCoy (CM), H. Marx (FMNH), W. E. Duellman (KU), R. L. Bezy and J. W. Wright (LACM), E. E. Williams (MCZ), H. W. Greene and D. B. Wake (MVZ), J. R. Dixon (TCWC), S. -K. Wu (UCM), P. Meylan (UF), A. G. Kluge and R. A. Nussbaum (UMMZ), W. R. Heyer and F. I. Irish (USNM), and William F. Pyburn (UTA). We are grateful to William E. Duellman, Darrel Frost, and Larry David Wilson for their thoughtful comments on the manuscript and to Rafael Joglar for translating the Spanish summary. Harry W. Greene kindly provided the photograph of *A. nigrilatus*. Finally, we express our debt of gratitude to Licenciado Mario Dary Rivera, the late Rector of the University of San Carlos, who was assassinated on December 15, 1981. He aided us in innumerable ways and always made our visits to Guatemala most memorable and pleasant. His wisdom, foresight, and sense of humor will be sadly missed.

RESUMEN

Una nueva especie de *Adelphicos* se describe de las tierras altas que flanquean el sureste de la Ciudad de Guatemala en el departamento de Guatemala. Esta especie poseé una escamación, coloración, y osteología distintiva y es notable por su gran tamaño. Un análisis de la variación morfológica de las poblaciones disyuntas de tierras altas de *Adelphicos* en el sur de México y Guatemala revelan diferencias consistentes de suficiente peso que justifican el reconicimiento de estas poblaciones como especies distintas. Estas especies juntamente con la especie que aquí se describe, constituyen un linaje monofilético conocido como el grupo *veraepacis*,

endémico a las tierra altas de el sur de México y el norte de Centro América.

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